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Minireview

Landscape genetics goes to sea

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Abstract

A recent study revealing geographical and environmental barriers to gene flow in the harbour porpoise shows the great potential of 'landscape genetics' when applied to marine organisms.

Analysis of the genetic structure of populations using molecular markers is currently undergoing a revolution as a result of the advent of novel conceptual and statistical developments, along with advances in molecular biology and genomics [1]. One of the most promising new avenues consists in combining information on geographical landscape features with analysis of molecular markers in order to understand how environmental factors affect the dispersal of individuals and the size and density of populations. This discipline, termed 'landscape genetics' [2,3], provides a bridge between landscape ecology and population genetics and has so far concentrated on terrestrial [4] and freshwater [5] organisms. The marine environment may superficially be conceived as coherent and homogenous across large geographical distances. Concordant with this view, several studies have shown significantly lower genetic differentiation among populations of marine fish species as compared to freshwater fishes [6]. Nevertheless, since the late 1990s, studies have increasingly documented genetic differentiation among populations of marine organisms, often coinciding with transitions between different basins [7,8] and gyres and eddies [9]. Landscape genetics may show particularly strong potential for determining the factors shaping these patterns of genetic structuring in marine organisms.

Barriers to gene flow in the harbour porpoise

In an interesting new study, Fontaine and colleagues [10] applied landscape-genetics methods to analyze the genetic structure of the harbour porpoise (*Phocoena phocoena*) over a geographical region ranging from the Black Sea to the northernmost parts of the eastern Atlantic. The study was based on analysis of microsatellite DNA variation in a total of 752 individuals. Fontaine *et al.* first used a well-established program, Structure [11], for determining the number of groups or populations represented by the sampled individuals. The results provided a strong signal for the presence of three genetically distinct groups, corresponding to harbour porpoise from the Black Sea, individuals from the Atlantic Ocean off the Iberian Peninsula, and individuals from a vast region comprising the eastern Atlantic north of the Iberian Peninsula. Application of a new individual-based landscape-genetics statistical method, Geneland [12], which partitions individuals into groups similarly to Structure but simultaneously takes the geographical location of sampled individuals into account, identified the same groups and suggested barriers to gene flow between these three geographical regions. This was further substantiated by a method for estimating real-time dispersal [13], which showed that virtually no gene flow occurs among groups. Finally, the authors demon-

strated significant isolation-by-distance (that is, a positive relationship between geographic distance and genetic differentiation) among harbour porpoise from the northern Atlantic range.

What makes the study particularly interesting is the detailed sampling scheme and the integration with oceanographic data, that is, landscape (or seascape) variables, making an explanation of the observed patterns of differentiation possible. It was known beforehand that the Black Sea population is probably reproductively isolated from Atlantic populations; harbour porpoise is absent from the Mediterranean Sea, and the Black Sea population is considered a relict of a more widespread population. However, the barrier to gene flow between the Iberian Peninsula and the northern part of the Atlantic is particularly noteworthy. This discontinuity coincides with a deep trough extending from the deep sea into the continental shelf in the southern Bay of Biscay, which has the effect of creating a zone of warm, oligotrophic (nutrient poor) water. Fontaine *et al.* [10] suggest that this zone provides an unfavorable habitat for the harbour porpoise, due in particular to its low productivity. In contrast to larger cetaceans, harbour porpoises have a limited capacity for energy storage, do not undertake long feeding migrations and largely depend on the food immediately available [14]. Thus, although the genetic break occurring in the southern Bay of Biscay is concordant with differences in sea-surface temperature, the ultimate cause is productivity, for which sea-surface temperature becomes a proxy. The absence of the species in the Mediterranean Sea coincides with similar environmental conditions, that is, deep water with high surface temperatures and oligotrophic conditions. Despite the difference in geographic scale, the factors isolating Iberian and Black Sea populations are therefore likely to be similar.

Even though strong barriers to gene flow were not observed within the northern Atlantic range, the significant isolation-by-distance suggests differentiation within a continuous population (see also [15]). Thus, the genetic structure of the harbour porpoise appears to reflect two types of factors: geographic distance (as in the northern Atlantic) and distinct discontinuities in the marine environment associated with low productivity.

Landscape genetics in marine environments

The work of Fontaine *et al.* [10] provides an excellent illustration of the increase in explanatory power that can be gained by integrating molecular data and oceanographic/landscape variables in studies of marine organisms. A handful of other studies have recently used similar landscape-genetics approaches to study both marine inver-

tebrates [16,17] and marine fishes [18-21]. Kenchington *et al.* [16] and Galindo *et al.* [17] studied sea scallops (*Placopecten magellanicus*) and staghorn corals (*Acropora cervicornis*), respectively, and combined information on the geographic location of barriers to gene flow with predictions of larval dispersal obtained from oceanographic models. Both studies showed that ocean currents influencing the dispersal of juvenile life stages were the most likely factors causing the observed genetic structure. In marine fishes, genetic breaks in Atlantic cod (*Gadus morhua*) around Iceland have also been related to prevailing ocean currents, suggesting that oceanic fronts may prevent gene flow between locations north and south of the island [20]. These results highlight the importance of ocean currents for shaping genetic structuring in species with pelagic egg and larval stages.

Other studies have related genetic breaks to specific environmental parameters. For instance, barriers to gene flow between geographically proximate Atlantic herring (*Clupea harengus*) populations in the Baltic Sea and North Sea coincide with marked changes in ambient salinity, suggesting that barriers are maintained through adaptation to local environments [18,19]. In this way, landscape genetics may provide important new information about the extent of local adaptation in marine environments, and the results can be used to formulate hypotheses that can then be tested using more targeted experimental approaches, for instance using standard or common-garden experiments [22].

Management of marine ecosystems

Landscape genetics is a rapidly evolving discipline, and the specific applications for marine environments are manifold. Management of marine living resources is increasingly shifting towards ecosystem-based management [23]. Using a comparative approach to landscape genetics involving analysis of several species may enable us to delimit geographic management units corresponding to barriers to gene flow shared by several species. The most important barriers to gene flow detected in studies of Atlantic herring and European flounder (*Platichthys flesus*) [18,19,21] are shown on a map of northern Europe (Figure 1). It is evident that the Baltic Sea includes an important genetic transition zone, even though the barriers detected in the two species in this region do not completely overlap. This may be due to patchiness within the spawning areas of herring, whereas the flounder shows a geographically more continuous spawning activity. When results from other species can be superimposed on this map, even more interesting patterns of coincident barriers might be revealed. It should also be noted that the barrier for harbour porpoise in the southern Bay of Biscay detected by Fontaine *et al.* [10] coincides with

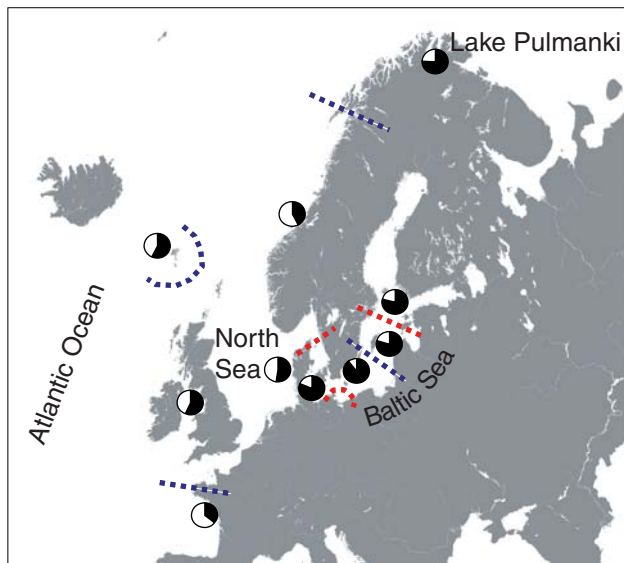


Figure 1

Barriers to gene flow detected in Atlantic herring and European flounder, along with the geographical distribution of frequencies of two alleles at the heat-shock protein gene *Hsc70* in the flounder. The map shows the main barriers (that is, zones of lowered gene flow) detected by analysis of microsatellite DNA markers in Atlantic herring [18,19] (red dotted lines) and European flounder [21,27] (blue dotted lines). The pie charts denote the frequencies of two alleles (indicated by black and white, respectively) at the *Hsc70* locus in the European flounder at the indicated locations [27].

a previously established border between biogeographic zones. Thus, the two genetically distinct harbour porpoise populations may in fact represent two at least partially independent ecosystems.

Another very promising use of landscape genetics relates to analysis of selection and local adaptation in marine environments. As described above, so far methods have mostly been used in an exploratory fashion to generate specific hypotheses, but recent developments hold much promise for more direct tests for selection using landscape-based approaches. These methods attempt to include information from specific environmental parameters in addition to the geographic position of the sampled individuals to identify potential selective agents involved in structuring populations and to identify loci subject to selection [24,25]. Even though the identification of specific environmental parameters as selective agents is challenging (see [21,26,27] for discussions), such techniques may prove particularly useful for marine organisms inhabiting regions that already have detailed oceanographic information.

As an example of the potential of a landscape-genetics approach to detecting selection, Hemmer-Hansen *et al.* [27]

analyzed variation in a heat-shock protein gene (*Hsc70*) in the European flounder. The frequencies of the two observed alleles are shown in Figure 1. Interestingly, there was a pronounced shift in allele frequencies between Baltic Sea and North Sea/Atlantic populations. There was, however, no correspondence between the barriers detected by neutral microsatellite DNA loci and the allele frequencies at *Hsc70*. In contrast, *Hsc70* allele frequencies were very similar among geographically distant samples sharing similar environmental conditions: that is, among all oceanic samples on the one hand and among samples from the Baltic Sea and Lake Pulmanki (a freshwater body connected to the sea) on the other. The latter group of samples is characterized by low salinity and low and fluctuating temperature regimes. Hence, the microsatellite loci suggest the presence of barriers reflecting zones of low dispersal and regions of high dispersal, whereas variation at *Hsc70* reflects strong diversifying selection due to differences in environmental conditions, sometimes even in the presence of considerable gene flow.

The work of Fontaine *et al.* [10], with its convincing correlation between population genetics and physical and ecological features of the marine environment, clearly confirms that landscape genetics has taken successfully to the oceans. We envisage that it will develop into an efficient research vessel with more and more scientists on board.

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